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Proximate Composition and Energy Density of Some North Pacific Forage Fishes

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ABSTRACT. Mature pelagic forage fish species (capelin, sand lance, squid) had greater lipid concentrations than juvenile age-classes of large demersal and pelagic fish species (walleye pollock, Pacific cod, Atka mackerel, greenling, prowfish, rockfish, sablefish). Myctophids preyed on by puffins have at least twice as much lipid per gram compared to mature capelin, sand lance and squid, and an order of magnitude greater lipid concentrations than juvenile forage fish. Energy density of forage fishes was positively correlated with lipid content, and negatively correlated with water, ash-free lean dry mass (mostly protein), and ash contents. COMP BIOCHEM PHYSIOL 118A;4:1393–1398, 1997. © 1997 Elsevier Science Inc.

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INTRODUCTION

During the past two decades, populations of several species of piscivorous marine birds and mammals have declined precipitously in the Gulf of Alaska (19). A number of hypotheses have been advanced to explain these declines. These include: (a) changes in the abundance and distribution of common fish prey (hereafter called "forage fish") owing to commercial fisheries or natural long-term changes in marine food webs (9,14); (b) unusual mortality of juveniles and adults from disease, or; (c) mortality from several anthropogenic sources (*e.g.*, oil spills, gill-nets, hunting).

Evidence suggests that the species composition and abundance of forage fish communities changed rapidly in the late 1970s, but it is not clear how these changes may be linked to declines in predator populations. One possibility is that different forage fish species have significantly different nutritional and energetic value. For example, lipid-rich capelin (*Mallotus villosus*) largely disappeared from seabird diets in the Gulf of Alaska by the 1980s, and were replaced by juvenile walleye pollock (*Theragra chalcogramma*), which have relatively low lipid content (12,19).

Except for a few commercially important species such as capelin and walleye pollock (11,12), however, little is known about the energetic value of forage fish in the North Pacific. In the Gulf of Alaska and Aleutian Islands, marine birds and mammals prey on a wide variety of pelagic schooling fishes (*e.g.*, Pacific sand lance [*Ammodytes hexapterus*], capelin) and juvenile age-classes of larger demersal species (*e.g.*, walleye pollock, Pacific cod [*Gadus macrocephalus*], etc.). In this study, we determined the proximate composition and energy density of a suite of forage fish found commonly in North Pacific seabird or marine mammal diets. These data should aid in understanding predator population declines, constraints on productivity, and be useful in models of marine energy dynamics (3,8,9).

MATERIALS AND METHODS

The fish used in this study were collected in July and August 1993–1994 while investigating trophic interactions at eight tufted puffin (*Fratercula cirrhata*) colonies ranging from Flat Island (56°, 48'N, 153° 45'W) in the southern Kodiak archipelago to Anangula Island (53° 00'N, 169° 53'W) in the eastern Aleutian Islands, following methodology described in detail by Hatch and Sanger (9). We sampled fish by placing screens over burrow entrances used by breeding puffins. Parents returning to provision their chick dropped fish at or near the blocked burrow entrance. Undamaged fish were collected within 2 hr, identified, weighed using Pesola spring scales (10 g ± 0.2 g; 50 g ± 0.5 g), and measured (total standard length, ±1 mm) before being individually bagged and frozen within 6 hr. We did not attempt to iden-

TABLE 1. Identification and morphometrics of forage fish species collected in Alaska during July and August of 1993 and 1994

Taxon	Common name	Sex*	Age†	N‡	Length (mm)		Wet mass (g)	
					Range	Mean	Range	Mean
Pleurogrammus monopterygius	Atka mackerel	U		5	70–71	70.5	2.8–3.7	3.1
Mallotus villosus	Capelin	F	2	4	100–113	105.3	5.9–6.7	6.3
Mallotus villosus	Capelin	M	2	5	110–118	114.2	7.7–9.8	9.0
Mallotus villosus	Capelin	U	1	5	80–92	85.9	2.0–2.9	2.4
Hexagrammos spp.	Greenling	U		4	55–70	61.8	1.2–2.8	2.2
Myctophidae§	Myctophid	U	4+	15	70–139	108.3	2.2–11.2	7.4
Gadus macrocephalus	Pacific cod	U		5	69–103	89.1	2.0–7.8	3.9
Trichodon trichodon	Pacific sandfish	U		4	80–95	88.8	3.0–9.1	6.3
Theragra chalcogramma	Walleye pollock	U	0	15	54–87	74.8	0.8–4.7	2.6
Zaprora silenus	Prowfish	U		5	95–132	113.0	9.7–28.8	17.1
Sebastes spp.	Rockfish	U		4	36–60	53.3	0.4–2.2	1.6
Anoplopoma fimbria	Sablefish	U		3	55–69	63.3	0.9–2.0	1.5
Ammodytes hexapterus	Pacific sand lance	F/U	2+	5	147–191	165.0	12.0–23.7	16.3
Ammodytes hexapterus	Pacific sand lance	U	1	12	110–132	122.0	3.9–8.4	5.8
Ammodytes hexapterus	Pacific sand lance	U	0	5	80–85	82.0	1.5–1.8	1.6
Gonatidae	Squid	U		9	71–135	97.2	3.5–12.3	7.7

*U-undetermined; F-female; M-male.

†Age determination of capelin, pollock, and sand lance based on length-age relationships cited from sources in: Hatch, S.A. & Sanger, G.A. (1992). Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar. Ecol. Prog. Ser. 80:1–14.

‡Sample sizes refer to individual fish that may have been pooled or split for lipid extraction (see Methods).

§Not consistently identified to genus or species, but most myctophids taken by puffins in the Gulf of Alaska are *Stenobrachius leucopsarus* (J.F. Piatt, unpubl. data). Myctophids were aged following length-age relationships determined for *Stenobrachius* in: Smoker, W. & Pearcy, W.G. Growth and reproduction of the lanternfish *Stenobrachius leucopsarus*. J. Fish. Res. Bd. Canada 27:1265–1275;1970.

tify species of myctophids (Myctophidae spp.) in our collection, but they were probably *Stenobrachius leucopsarus*, based on historical measures of abundance (2,24) and prevalence in Bering Sea and Aleutian Island kittiwake (*Rissa* spp.) and murre (*Uria* spp.) diets (23). Breeding capelin and sand lance were sexed based on external morphology. Where possible, specimens were aged following published length-age relationships (Table 1). Specimens were kept frozen at −20°C until analysis.

In the laboratory, specimens were weighed on an analytical balance (±0.1 mg) to determine wet mass. The specimen storage bags contained small amounts of water that we accounted for by drying both specimens and preweighed bags to constant mass in a convection oven at 60°C, then reweighing to determine water content (Table 2).

Lipid content of the dried, homogenized specimens was determined by solvent extraction using a Soxtec HT-12 soxhlet apparatus with hexane/isopropyl alcohol 7:2 (v:v) as the solvent system. This extracts neutral (storage) lipids (triglycerides and wax esters) and complex structural lipids (phospholipids, sterols, etc.) without extracting nonlipids (20). We extracted total lipids because we were interested in the nutritional value of the fish samples, not just their stored energy reserves. Specimens were combined or split, as required, to achieve a dry sample mass for extraction of 1.0–3.5 g. Lean dry samples were transferred from extraction thimbles to glass scintillation vials and ashed in a muffle furnace at 550°C for 24 hr in order to calculate ash-free lean dry mass [*ca.* 94% protein; (17)] by subtraction.

Specimen energy densities (kJ/g) were calculated on a dry mass basis from their composition using published energy equivalents of lipid and protein for uricotelic vertebrates [39.3 kJ/g and 17.8 kJ/g, respectively (21)], assuming that ash-free lean dry mass (AFLDM) consists only of protein. Carbohydrates have been shown to be an insignificant component of fish [<0.6%; (6)] and were ignored in our analysis. Energy densities on a wet mass basis were calculated from water percentage (10) as: dry energy density × (1-proportion of water).

RESULTS AND DISCUSSION

Water content ranged from 71% in myctophids to 86% in prowfish (*Zaprora silenus*) (Table 2, Fig. 1), and was negatively correlated with lipid content ($r^2 = 0.635$, $P < 0.001$, $N = 68$). Lipid content varied widely, from 6% of dry mass in juvenile Pacific cod and sand lance to 53% in myctophids (Table 2). AFLDM ranged from 40% of dry mass in myctophids to 80% in age-class 0 sand lance, but was between 70 and 80 percent for 9 of 12 species (Fig. 1). Ash content varied from 7% of dry mass in myctophids to 22% of dry mass in rockfish (*Sebastes* spp.) and sablefish (*Anoplopoma fimbria*).

Dry energy densities varied between 16 kJ/g in rockfish and sablefish and 28 kJ/g in myctophids (Table 3, Fig. 1). Differences in water content amplified the range of energy densities when calculated on a wet mass basis, from 2.4 kJ/g in prowfish to 8.1 kJ/g in myctophids. Considering data

TABLE 2. Composition of forage fish species collected in Alaska during July and August of 1993 and 1994, by mean (± SD) percentage

Species (sex, age*)	Of wet mass				Of dry mass		
	Water	Lipid	Ash-free lean dry†	Ash	Lipid	Ash-free lean dry†	Ash
Atka mackerel	78.30 ± 0.32	2.96 ± 0.58	15.67 ± 0.27	2.71 ± 0.02	13.84 ± 2.52	73.46 ± 2.26	12.70 ± 0.26
Capelin (F,2)	77.81 ± 1.01	4.79 ± 0.67	15.28 ± 0.46	1.78 ± 0.11	21.87 ± 2.14	69.97 ± 2.27	8.16 ± 0.45
Capelin (M,2)	81.32 ± 1.20	2.69 ± 0.98	13.69 ± 0.30	2.04 ± 0.13	14.38 ± 4.27	74.53 ± 4.19	11.09 ± 0.49
Capelin (1)	75.49 ± 1.32	4.19 ± 0.70	17.65 ± 0.82	2.39 ± 0.01	17.25 ± 1.82	72.89 ± 1.15	9.86 ± 0.66
Greenling	79.33	1.78	15.13	3.41	8.75	74.48	16.77
Myctophid	71.24 ± 2.72	14.68 ± 1.97	10.96 ± 0.73	1.96 ± 0.23	53.00 ± 2.35	39.83 ± 1.61	7.18 ± 1.30
Pacific cod	81.89 ± 0.65	0.98 ± 0.13	13.97 ± 0.87	2.72 ± 0.21	5.55 ± 0.88	79.01 ± 2.52	15.44 ± 1.64
Pacific sandfish	80.42 ± 0.03	1.67 ± 0.50	14.88 ± 0.41	2.72 ± 0.20	8.65 ± 2.57	77.24 ± 2.05	14.11 ± 1.06
Walleye pollock	83.74 ± 0.60	1.44 ± 0.54	11.84 ± 0.49	2.66 ± 0.56	8.99 ± 3.24	74.31 ± 1.39	16.71 ± 3.67
Prowfish	86.46 ± 0.28	1.43 ± 0.18	9.87 ± 0.31	1.87 ± 1.94	10.77 ± 1.29	74.57 ± 0.62	14.66 ± 1.15
Rockfish	81.39	1.74	12.33	3.99	9.61	68.31	22.09
Sablefish	83.06	1.30	11.69	3.66	7.83	70.17	22.00
Pacific sand lance (2+)	73.22 ± 2.01	6.49 ± 1.47	17.25 ± 0.55	2.81 ± 0.43	24.25 ± 3.67	65.21 ± 4.15	10.54 ± 1.15
Pacific sand lance (1)	75.45 ± 2.03	4.74 ± 1.68	16.82 ± 0.77	2.51 ± 0.28	19.32 ± 5.64	70.14 ± 4.07	10.54 ± 1.75
Pacific sand lance (0)	80.90	1.18	14.87	2.62	6.32	79.66	14.02
Squid	81.61 ± 0.90	3.65 ± 0.72	12.78 ± 0.93	1.49 ± 0.15	20.41 ± 4.03	71.29 ± 3.63	8.30 ± 0.70

Species shown without SD were pooled into a single sample for lipid extraction.

*F = female; M = male; number = fish age-class.

†Ca. 94% protein (Montevecchi et al. Growth energetics of nestling Northern Gannets (Sula bassanus). Auk 101:334–341;1984).
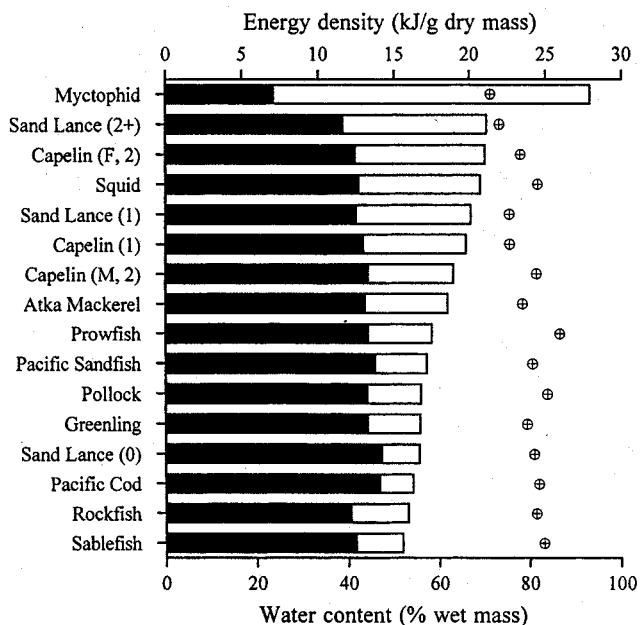
FIG. 1. Total energy densities (kJ/g dry mass) of forage fish species collected in the Gulf of Alaska and Aleutian Islands. Values are ranked in descending order and show relative energy contributions of ash-free lean dry mass (black bar) and lipid (white bar) in 12 forage fish species, including different sex (M,F) and age-classes (0, 1, 2+) of capelin and sand lance. Fish lengths range from 36–191 mm (Table 1). Water contents (circles) are shown to illustrate the inverse relationship ($r^2 = 0.645$, $P < 0.001$, $N = 68$) with energy densities. See Table 1 for scientific names of fish.

pooled from all species, dry mass energy density was positively correlated with lipid content ($r^2 = 0.986$, $P < 0.001$, $N = 68$), and negatively correlated with AFLDM ($r^2 = 0.901$, $P < 0.001$, $N = 68$), ash ($r^2 = 0.640$, $P < 0.001$, $N = 68$), and water content ($r^2 = 0.645$, $P < 0.001$, $N = 68$). Energy density of wet mass was more strongly correlated with water content ($r^2 = 0.892$, $P < 0.001$, $N = 68$).

A general pattern emerged from these results. Juvenile age-classes of large demersal and pelagic fish species (walleye pollock, Pacific cod, Atka mackerel [*Pleurogrammus monopterygius*], Pacific sandfish [*Trichodon trichodon*], prowfish, greenling [*Hexgrammos* spp.], sablefish, rockfish) tended to be low in lipid content and consequently low in energy density, whereas the pelagic schooling species capelin, squid (Gonatidae spp.), and sand lance were higher in lipids and therefore had high energy densities. Myctophids were extraordinarily rich in lipids, and had the highest energy density of all forage fish species examined. We caution that because our samples were all taken within a narrow time frame, and each fish species varies seasonally in fat content (15), our results should not be applied uncritically to other times of year (10).

Mean lipid concentrations of myctophids determined in this study (Table 2) compare favorably with those reported for *S. leucopsarus* by Nevenzel *et al.* [56.4% of dry mass, *N* = 17 (18)] and Childress and Nygaard [13.1% of wet mass (5)]. Butler and Pearcy (4) reported a higher value (59.8% of dry mass, *N* = 28), but as noted by Childress and Nygaard (5) the discrepancy may stem from different extraction techniques since Butler and Pearcy (4) used chloroform:methanol 2:1 as the solvent system, which extracts appreciable nonlipid material (7). The solvent system used in the present study was chosen to minimize extraction of nonlipid components (20). Nevenzel *et al.* (18) found neutral lipids in *S. leucopsarus* comprised 92% of total lipids (91% wax esters, 1% triacylglycerols).

Our sample of myctophids included one exceptionally lean individual (length 150 mm, 88% water) whose lipid content was only 13% of dry mass and 1.5% of wet mass. This may have been *Lampanyctus regalis*, whose lipid content was reported by Butler and Pearcy (4) to be 16.6% of dry mass. Smoker and Pearcy (22) only found evidence of spawning in *S. leucopsarus* from December to March, so it is unlikely that this individual was a spawned-out female *S. leucopsarus*. Due to uncertainty over its species identification and aberrantly high water content, we removed it from all analyses.

Our results are in rough agreement with the limited data available on sand lance (Tables 2 and 3). Ackman and Eaton (1) found commercially caught Atlantic sand lance (*Ammodytes americanus*, presumably age-class ≥ 2) to contain a mean of 7.2% oil (80% triacylglycerol, 9.4% phospholipid), and Krzynowek and Murphy (12) reported sand lance (*A. americanus*) contained 7.2% "fat" (both measurements on a wet mass basis). Montevecchi *et al.* (17) reported sand lance (*A. hexapterus*) contained 8.9% lipid, equivalent

TABLE 3. Energy densities of forage fishes sampled in Alaska

Species (sex, age†)	Energy density (kJ/g ± SD)*	
	Dry mass	Wet mass
Atka mackerel	18.52 ± 0.59	4.02 ± 0.19
Capelin (F,2)	21.05 ± 0.45	4.67 ± 0.31
Capelin (M,2)	18.92 ± 0.94	3.54 ± 0.41
Capelin (1)	19.75 ± 0.51	4.84 ± 0.39
Greenling	16.70	3.45
Myctophid	27.92 ± 0.70	8.05 ± 0.94
Pacific cod	16.25 ± 0.10	2.94 ± 0.12
Pacific sandfish	17.15 ± 0.69	3.36 ± 0.13
Walleye pollock	16.76 ± 1.33	2.73 ± 0.26
Prowfish	17.51 ± 0.47	2.37 ± 0.08
Rockfish	15.93	2.97
Sablefish	15.57	2.64
Pacific sand lance (2+)	21.14 ± 0.76	5.67 ± 0.61
Pacific sand lance (1)	20.08 ± 1.50	4.95 ± 0.74
Pacific sand lance (0)	16.66	3.18
Squid	20.71 ± 0.95	3.81 ± 0.24

Note. Species shown without SD were pooled prior to lipid extraction.
*See Methods for calculations.
†F = female, M = male; 0,1,2,2+ = fish age-class.

to 7.3 kJ/g wet mass. Using bomb calorimetry, Hislop et al. (10) found age-class 0 sand lance (*A. marinus*) averaged 20.56 kJ/g dry mass, while age-class 1 specimens averaged 22.33 kJ/g dry mass and age-class 2+ averaged 23.01 kJ/g dry mass, similar to our data in terms of increasing energy density with age. Their 10–15% higher values (Table 3) are probably due to the fact that bomb calorimetry includes nonassimilable body components in energy density determination.

Capelin have been relatively well studied, with extensive data available on composition and energy density of mature specimens (15). Our determination of energy density in mature capelin is similar to the mean energy density of wet mass (4.5 kJ/g) reported in Montevecchi and Piatt (15) for mature specimens caught in summer. Previously reported lipid content of immature capelin was much lower [mean of 1.1% of wet mass; length range 100–130 mm; (25)] than the mean value for our age-class 1 capelin (length range 80–92 mm), although this may be a seasonal effect because the values reported by Winters (25) were from fish collected in late winter and spring.

Squid showed relatively high lipid levels on a dry mass basis, but were also high in water and, therefore, have moderate energy density on a wet mass basis; comparable to the 4.3 kJ/g found in squid (*Ilex illecebrosus*) fed to seabird chicks in Newfoundland (17). All other species examined in our study were juveniles, and were comparable to juvenile capelin; being high in water content and low in lipid content, resulting in low energy densities (Tables 2, 3, and Fig. 1).

We found energy density increased with age among both capelin and sand lance, consistent with other studies showing juveniles with lower lipid reserves than even spawned-out mature females (10,11,25). Mature male capelin, with lower energy densities than age-class 1 capelin, were an exception to this trend. Lipid reserves of spawning males, however, may be diminished to a greater extent than females' reserves, due to a greater spawning effort by males (13,15,25).

We examined the relationship between fish standard length and energy density, but found the correlation to be nonsignificant in the majority of species. We have little confidence in the negative results, however, due to small sample sizes and confounding effects of season and location. Three species groups did show significant positive correlations between length and dry energy density: myctophids ($r^2 = 0.324$, $P < 0.05$, $N = 13$, range 70–139 mm), age 2+ capelin ($r^2 = 0.568$, $P < 0.05$, $N = 9$, range 100–118 mm), and juvenile pollock ($r^2 = 0.875$, $P < 0.05$, $N = 5$, range 54–87 mm).

The negative correlation between water and lipid content in fish may provide a quick and cost-effective index to relative energy content by measuring water content (10). There were, however, several species in our sample whose water content was exceptionally high (prowfish, squid; Fig. 1), which would result in underestimations of dry energy

densities relative to other species. Thus, water content may serve as a useful index to energy density only within species.

We join past workers in calling for standardization of proximate composition and energy density data (10,16). These data are most appropriately compared on a dry mass basis because of problems in accounting for water loss from fish specimens prior to analysis. Caution is required in comparing wet mass energy densities across studies: whereas we found age-class 1 capelin had a lower energy density than gravid female capelin when expressed on a dry mass basis, they had a higher energy density when expressed on a wet mass basis. This discrepancy probably results from exceptional desiccation of the age-class 1 capelin prior to freezing, thereby artificially inflating the wet energy density values. However, important ecological questions (provisioning costs to parents; total energy delivered to young, etc.) can only be addressed using wet energy density. More studies using carefully preserved and promptly analyzed fishery samples (10) would clarify wet vs dry mass energy density relationships.

A further point of confusion in past energetic studies has been the methods and energy equivalents used to calculate energy density. Bomb calorimetry is generally inappropriate for nutritional studies, because it measures the energy content of nonassimilable components and therefore overestimates the amount of energy actually available to fish consumers. In the present study, we use composition data together with the energy equivalents most appropriate for birds, representing the total energy a bird is able to metabolize from a given amount of fish. Other workers may decide to use different equivalents for other predator groups (e.g., fish or mammals), or to pursue different avenues of analysis, emphasizing the need to consistently present energy density data in conjunction with its source proximate composition data.

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